

# Ecosystem type differences in nitrogen process rates and controls in the riparian zone of a montane landscape

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## Abstract

Nitrogen (N) inputs to the world's aquatic ecosystems have increased over the past 100 years. Riparian zones and other wetlands are known to remove N from ground and surface waters before they enter lakes and streams. However, the effect of riparian wetlands on water quality has been shown to differ dramatically among sites. Sources of landscape variation in riparian N dynamics have been poorly documented and rarely quantified. Within the Lake Tahoe Basin (LTB), we hypothesized that differences in riparian N dynamics correlate to differences in ecosystem type. To test this hypothesis, we randomly selected 20 plots, four each of five ecosystem types, along a tributary to Lake Tahoe. Throughout the snow-free season, we measured soil N transformations and groundwater chemistry in each plot. We found significant differences in denitrification potential, net mineralization, net nitrification and groundwater nutrient flux among different ecosystem types. These results suggest that classification of riparian zones into ecosystem types might be useful in predicting landscape differences in riparian water quality effects.

We also tested for factors expected to directly and indirectly control riparian N process rates using data collected at each study site. Using correlation and multiple regression analysis, we found that N process rates were most highly correlated with different control factors according to ecosystem type. Differences in direct and indirect control factors among ecosystem types indicate that construction of mechanistic, landscape models of riparian processes might be most accurately done by stratifying the riparian zone into ecosystem types rather than by viewing it as a single, homogeneous part of the watershed.

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## 1. Introduction

Past studies in agricultural regions of the U.S. and Europe show that over 90% of anthropogenic nitrogen (N) in groundwater can be removed as water moves through riparian zones to the stream channel (e.g. Peterjohn and Correll, 1984). Although riparian N dynamics have been studied in a wide array of low elevation landscapes, relatively little is known about how these processes affect ground and surface water quality in mountainous regions. Water quality in many mountainous areas is threatened by changes in human land use and increases in atmospheric nitrogen (N) deposition (Byron et al., 1990; Cahill et al., 1996; Peterson et al., 1987; Stoddard, 1994). Therefore, a better

understanding of how mountain riparian zones affect ground and surface water quality is needed to inform restoration, land management and conservation decisions.

Spatial variation in riparian nutrient dynamics is not well understood in low elevation landscapes and rarely studied in mountainous riparian ecosystems (Hussey et al., 1985; Ashby et al., 1998). Denitrification is a process by which added N can be removed from the soil/groundwater system; therefore, this process can be a critical in maintaining or recovering high water quality in areas subject to excess N input. Past research has shown that large variation in riparian denitrification is related to fine scale shifts in topography, soil texture, soil organic matter, groundwater flow paths and chemistry and variation in plant species composition (e.g. Ettema et al., 1999; Hedin et al., 1998; Jacinthe et al., 1998). However, integrated measures of more distal process controls are required to develop watershed scale models needed for land management and policy decision-making. Several landscape scale variables have been examined

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as possible indicators of variation in riparian denitrification, including soil drainage class (Nelson et al., 1995) and soil type (Pinay et al., 2000; Hill and Cardaci, 2004). Authors report significant differences in N dynamics associated with these two variables; however, they also describe important effects of fine scale variation in both soil texture and drainage on denitrification that would be very difficult to extend to the landscape scale. Ecosystem type is an integrative variable that can be mapped at the landscape scale. This variable has not yet been tested as a tool for identifying riparian areas with different soil and groundwater N effects.

In the montane landscape of Lake Tahoe Basin, we explored the utility of using riparian ecosystem types as integrators of fine scale variation in microbial N dynamics. The ecosystem type classification applies a state factor approach (sensu Jenny, 1980) by integrating information on landform and more site-specific soil and vegetative characteristics. The primary goal of this research is to determine if differences in riparian ecosystem type can be used to identify areas in the riparian zone that have significantly different N process rates and/or N process controls. We place greatest emphasis on denitrification, since this process directly removes N from the soil/water system. A secondary goal is to use correlation and step-wise regression analysis to identify

site characteristics that exert proximal and distal control over denitrification in the riparian zone.

## 2. Background

The riparian zone includes the area of groundwater, stream water interface, the soil–stream interface and the surrounding area of stream influence (Gregory et al., 1991). In upland ecosystems, climate, plant community type, disturbance and soil type are the major distal controllers of nitrification and denitrification (Robertson, 1989). In the riparian zone, findings from past research indicate that the hydrologic structure of the streamside environment provides the physical template that controls N dynamics (Hill, 1996). As detailed in Fig. 1, we expect that differences in the hydrologic setting can affect three proximal controllers of denitrification, which include oxygen, inorganic N and C availability (Robertson, 1989). Characteristics of the hydrological setting, such as channel form and geofluvial surface, reflect important hydrologic and geomorphic processes including erosion, deposition, meandering and down cutting (Knighton, 1984), and are directly related to frequency and duration of flooding (Wolman and Leopold, 1957). Flood frequency, intensity and duration affects soil texture and soil moisture

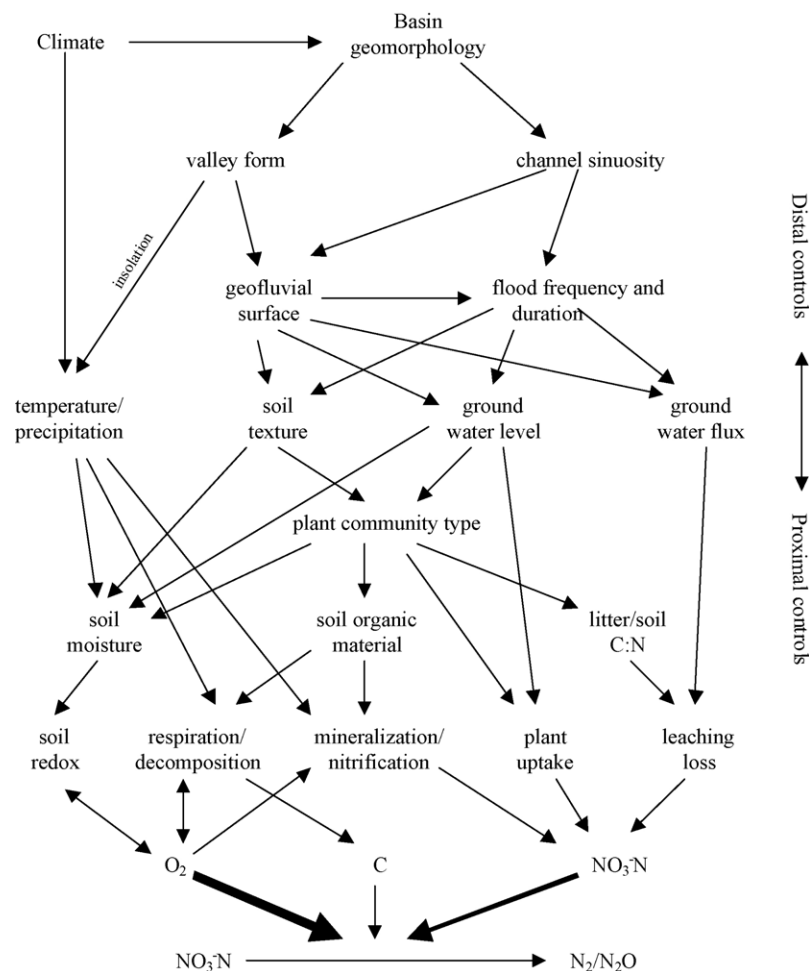


Fig. 1. Flow diagram reflecting proposed proximal to distal controls on microbial denitrification in the riparian zone. This figure was adapted from Robertson (1989).

availability (Hupp and Osterkamp, 1985; Osterkamp and Hupp, 1984), which in turn affects soil aeration and oxygen availability. Similarly, depth to groundwater is expected to affect surface soil moisture, either through direct saturation when groundwater levels are at or above the surface, or through capillary fringe effect when soil is near the surface (Fig. 1). Soil saturation affects all microbial processes, including decomposition and microbial N and C uptake (Paul and Clark, 1989; Stark and Firestone, 1995). By limiting oxygen availability, high soil moisture content can suppress nitrification, thereby reducing local nitrate production, but can promote denitrification of imported nitrate (Cosandy et al., 2003; Pinay et al., 2000; Robertson, 1989; Paul and Clark, 1989). High soil moisture content can also promote DIN loss via leaching. Therefore, N and C availability is expected to vary with soil moisture content. Thus, we expect that the streamside hydrologic setting acts as an important distal controller of soil nitrification and denitrification, particularly through its effects on geofluvial surface, groundwater flow and soil moisture content (Fig. 1).

In the Tahoe Basin, we found that variables thought to strongly affect the hydrology of a riparian area (valley width, channel width and sinuosity, parent material and geofluvial surface) are also principle correlates with riparian ecosystem type (Merrill, 2001). These findings suggest that one might be able to use riparian ecosystem types to organize the landscape into areas with similar hydrologic settings and, therefore, into areas that might function similarly with respect to N cycling and removal. Differences in ecosystem type have been shown to reflect landscape variation in upland N dynamics (Zak et al., 1986; Merrill and Zak, 1992). Groffman et al. (1996) report significant differences in microbial biomass and N dynamics among isolated wetland types (e.g. fens, meadows and woodland pools). In order to test the hypothesis that differences in microbial N dynamics occur among riparian ecosystem types, we examined N dynamics in five ecosystem types identified in the Tahoe Basin (Merrill, 2001). All of the study sites were located along one of the least disturbed tributaries to

Lake Tahoe so that our findings could inform land managers of background conditions for wetlands restoration and conservation projects (Brinson and Rheinhardt, 1996). The five types represent common riparian ecosystems and range from steep alder shoots to sedge meadows in depositional reaches. Within each site, we measured potential denitrification, net mineralization, net nitrification, soil N pools and groundwater DIN flux. In order to test specific hypotheses that the hydrologic setting indirectly affects denitrification as outlined in Fig. 1, we also measured a suite of environmental variables, including factors expected to act as proximal and distal controls.

### 3. Methods

#### 3.1. Site description

This research was performed in Ward Creek Valley, one of the largest and least disturbed watersheds in the Lake Tahoe Basin (LTB) (Fig. 2). Elevations in the 2510 ha watershed span from 1898 m at lake level to 2700 m at the ridge tops. The majority of precipitation falls as snow, and adds up to 80 cm at lake level and to 160 cm or more at the ridge tops (Oregon Climate Service and PRISM Services, 1997). Average annual temperatures range from 6.2 to  $-2^{\circ}\text{C}$  and the growing season lasts for 2–3 months (July to August/September; NWS, 2000). Like much of the northern part of LTB, Ward Creek watershed is underlain by volcanic andesites and glacial till. Most water enters Ward Creek as shallow subsurface flow (Coats, 1975). Ward Creek has three perennial headwater streams, all of which flow from alpine meadows situated in wide depositional valleys at the bases of glacial cirques. These upper-reach riparian areas are underlain by deep organic-rich soils that support a luxuriant growth of forbs, graminoids and patches of riparian shrub. A stream continuum that flows to Lake Tahoe from the southernmost fork was sampled. This channel emerges from a talus slope and flows north through a high elevation meadow at a 1–4% gradient. A narrow, V-shaped valley confines the mid-reach

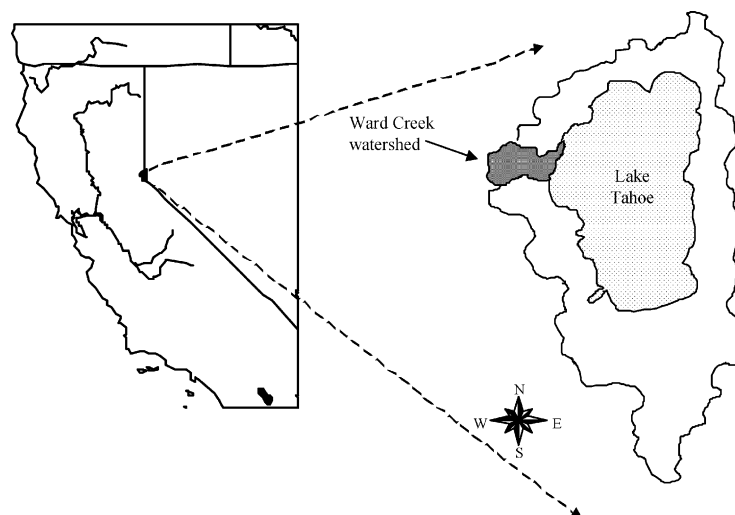


Fig. 2. This research was performed in the Lake Tahoe Basin, located on the border of California and Nevada, USA. Research plots were established along Ward Creek, a relatively undisturbed watershed on the northwestern shores of Lake Tahoe.

Table 1  
Characteristics of riparian ecosystem types examined in this study

Ecosystem type	Dominant species	Soil texture	Watershed position
Alders (A)	Thinleaf alder-sedge	Silt loam	Upper alluvial valleys
Upper Meadows (UM)	Sedge-corn lily	Sandy loam	Upper alluvial valleys
Transports (T)	Thinleaf alder-bishops cap	Sandy loam	Steep mid-reaches
Depositional Willows (DW)	Lemon's willow-wet sedge	Sandy loam	Lower wide alluvial valleys
Depositional Meadows (DM)	Grass-mesic forb	Sandy loam	Lower wide alluvial valleys

Soil textures reported from the upper 10 cm and measured using the hydrometer method of estimating percent sand, silt and clay (four plots per ecosystem type and four samples per plot). Textures determined using USDA soil triangle.

riparian zones of the south fork to a 4–7 m wide strip. These communities are dominated by riparian shrubs, and have an intermittent ground cover of forbs and graminoids. The mid-reach channel bottoms are composed of cobbles and boulders and flow northeast at 15–25% gradients. Farther downstream, the three tributaries merge into the main stem of Ward Creek. The lower depositional zone of Ward Creek meanders through a >500 m wide valley, filled with glacial till of primarily volcanic origin. Snowmelt tributaries and variously vegetated back channels intersect terraces supporting cottonwood-lodgepole forests and riparian meadows. The lower reaches of Ward Creek have gravel and sand beds and flow east along a 1–2% gradient.

### 3.2. Site selection and sampling strategy

Along Ward Creek, polygons supporting riparian ecosystems were delineated and numbered on aerial photographs. From a total of 56 such polygons, four polygons of each of five ecosystem types were randomly selected for further study. Within these polygons, 20 research plots along Ward Creek were established, with four replicate plots for each of five ecosystem types (Table 1). These five ecosystem types were identified through the ecosystem type classification described in Merrill (2001). For convenience, shorter names than those introduced in Merrill (2001) were used for each of the ecosystem types in this paper. The Alder (A) ecosystem type refers to type 6, the *Alnus/Mitella* banks. The Upper Meadow (UM) ecosystem type refers to the type 4, the *Veratrum/Carex* meadows. The Transport (T) ecosystem type refers to type 9,

the *Alnus-Salix/Athyrium* banks. The Depositional Willow (DW) ecosystem type refers to type 3, the *Salix/Ribes* back channels and the Depositional Meadow (DM) ecosystem type refers to type 2, the *Sidalcea/Poaceae* meadows.

In order to accommodate the interannual and elevational differences in weather, sampling was conducted according to plant phenology, rather than by the Julian calendar date. Spring sampling was initiated when riparian forbs (e.g. *Veratrum californicum*, which occurs in nearly all sites) were 5–10 cm high. Summer sampling began when annual grasses set seed; and fall sampling began when over half of the deciduous shrub leaves were senescent.

### 3.3. Experimental design

During the spring and summer of 1997, four sub-samples were collected from each of these 20 research plots and analyzed for potential denitrification as well as gravimetric soil moisture content. Repeated measures of soil N and C dynamics, groundwater level and N concentration, surface soil moisture, temperature, redox and soil oxygen content were collected, four sub-samples per plot, during the spring, summer, and fall of 1998, and the spring and summer of 1999. The sampling schedule is presented in Table 2. All soil analyses were performed on the top 10 cm of soil since past studies and preliminary sampling for this project demonstrated that soil microbial activity is highly concentrated in this upper layer of soil (Ambus and Lowrance, 1991; Lowrance, 1992; Ambus, 1993; Merrill, unpublished data).

Table 2  
Sampling schedule for measuring potential denitrification rates, net mineralization and nitrification rates, DIN pools, groundwater DIN concentrations and fluxes, and site characteristics during the 1997–1999 field seasons

Measurement	1997			1998		1999	
	June	September	July	August	September/October	June/July	August
Denitrification potential	•	•	•	•	•	•	•
Net mineralization			•	•	•		
Net nitrification			•	•	•		
DIN pools			•	•	•	•	•
Groundwater level			•	•	•	•	•
Groundwater chemistry			•	•	•	•	•
Microbially available C						•	•
Soil moisture content	•	•	•	•	•	•	•
Soil redox			•	•	•	•	•
Soil atmosphere O <sub>2</sub>			•	•	•		
Soil temperature			•	•	•		

### 3.4. Measurements of environmental variables

#### 3.4.1. Groundwater level

During 1997, the hardware needed to develop maps of the hydrologic setting of each research plot was installed. Within each 50 m<sup>2</sup> study plot, four wells and three or more piezometers were installed. In order to build three-dimensional maps of groundwater flow through these plots, a laser field transit (Criterion, Laser Technology Inc.) was used to measure the *x*, *y* and *z* coordinates of each well and piezometer relative to a single known position in each plot. Wells and piezometers were sunk 1.25 m or more below the surface. Wells were constructed out of 5 or 2 cm inner-diameter (i.d.) schedule 40 PVC that was slotted to 15 cm below the soil surface. Unslotted 2 cm i.d. schedule 40 PVC was used for the piezometers. Ventilated caps were placed on all wells and piezometers. Depth to groundwater was calculated by subtracting the above ground well height and wet height, or water line, from the total well length.

#### 3.4.2. Collection and analysis of groundwater samples

Wells and piezometers were drained and allowed to equilibrate for a minimum of 4 weeks prior to preliminary sampling in 1997. On each sample date, groundwater levels were measured, then each sample well was completely drained or, in case of very rapid recharge, four times the well's volume was removed. Clean nalgene tubing and clean plastic syringes (60 ml) equipped with three-way stopcocks were used to draw water samples from those wells that had over 7 cm of water. Each sample was immediately pressed through a pre-combusted glass microfibre filter (Whatman GF/F) into clean nalgene sample bottles. Samples were filled to the brim to eliminate NH<sub>3</sub> degassing into the bottle headspace. Samples were kept cool on snow or ice and frozen within 8 h of collection. Groundwater concentrations of ammonium and nitrate were measured using colorimetry on a Lachat autoanalyzer (FIA + 8000 Series). The salicylate-hypochlorite colorimetric method was used for ammonium analysis (Quikchem 10-107-06-2-B, Lachat Instruments), and the copperized cadmium reduction method was used for nitrate analysis (Quikchem 10-107-05-1-O, Lachat Instruments). Detection limits were  $\pm 2$   $\mu$ g/l. On each sample date, new sample bottles and tubing were used to collect groundwater samples. Syringes, filter holders, and stopcocks were reused after they had been rigorously cleaned, acid washed four times (7% HCl), and rinsed eight times with 18 megaohm deionized water. The tubing, syringes, filters and sample bottles were also rinsed with sample prior to collecting the final groundwater sample. Ground and surface water samples were collected throughout the spring, summer and fall of 1998 (Table 2).

#### 3.4.3. Hydraulic conductivity

Saturated hydraulic conductivity of soils in each study plot was measured using the constant-head method on repacked soil columns (Black, 1965). Cores were packed into 5 cm diameter  $\times$  20 cm long plastic sleeves. Packed soil columns were then soaked in water overnight to ensure complete

saturation. The following day, a constant head (5 cm) water column was established over each core and water that drained through the soil core within 3 min intervals was weighed. Each measurement was repeated three times to ensure consistency. These core averages were then combined into plot averages and applied to the model described below.

#### 3.4.4. Modeling groundwater flow and chemistry

A three-dimensional computer simulation model was developed to reflect saturated groundwater flow (*Q*) based on the Darcy equation (Dunne and Leopold, 1978):

$$Q = \frac{KA\Delta H}{L}$$

*Q* is the groundwater flow rate (m<sup>3</sup>/h); *K* the saturated hydraulic conductivity (m/h); *A* the cross-sectional area (set at 1 m<sup>2</sup>);  $\Delta H$  the difference in hydraulic head and *L* is the distance water travels through soil column.

The *x*, *y* and *z* coordinates of each well and piezometer were used to place them in a three-dimensional grid developed for each plot. For each plot on each measurement date, piezometer readings were used to define the piezometric surface, which made it possible to estimate the difference in hydraulic head ( $\Delta H$ ) between any two points on that plane. These data were used to estimate *Q* and to identify the dominant direction of groundwater flow for each treatment site on each measurement date. Groundwater N flux (mg N/h) for each sample well was calculated as the product of groundwater flow rate (m<sup>3</sup>/h) and groundwater N concentration ( $\mu$ g/l). Thus, given the groundwater flow rate and three or more points with known groundwater N concentrations, a coarse contour map showing N flux levels in each plot at each date was developed. We used contour maps of the piezometric surface of each 50 m<sup>2</sup> plot on each sample date to aid in interpreting these results.

#### 3.4.5. Soil atmosphere oxygen content

Approximately 100 soil atmosphere diffusion chambers (SAC's) were constructed according to Faulkner and Richardson (1989), using 5 cm schedule 40 PVC caps and 21 cm copper wires. Four SAC's were installed per site during fall 1997; however, many SAC's, particularly those in the Depositional Meadows, were broken by the heavy 1997–1998 snowpack and had to be replaced in early spring 1998. Air in the installed SAC's was allowed to equilibrate with the surrounding soil atmosphere for 2 or more weeks after installation. On each sample date, gas samples were collected from the SAC's using a three-way stopcock and 40 ml nalgene syringe. Gas samples were stored in pre-evacuated 30 ml jars sealed with rubber butyl stoppers. These samples were analyzed for oxygen content using thermal conductivity gas chromatography at U.C. Berkeley.

#### 3.4.6. Surface soil redox

Surface soil redox was measured in replicate at four points within each plot using constructed redox probes (Faulkner and Richardson, 1989) and a portable millivolt meter with a

saturated calomel reference electrode. In the field, each probe was inserted to 7–10 cm depth and allowed to equilibrate for 15 min before redox measurements were taken.

#### 3.4.7. Surface soil gravimetric moisture content and temperature

Field thermometers, inserted in the soil to 7 cm depth, were used to measure surface soil temperature at four points in each plot during the time of sampling (between 10 a.m. and 5 p.m.). Soil gravimetric moisture content was measured by comparing the before and after weight of samples dried for 24 h in a 105 °C oven (Faulkner and Richardson, 1989).

#### 3.5. Microbially available C

Available C pool size and respiration rate constants were determined by measuring microbial C respiration in 6-week incubations at U.C. Berkeley (Townsend et al., 1997). Four soil samples were collected from each plot. From these, 10 g of field moist soil was incubated in an air-tight one quart mason jar for 6 weeks during the spring and summer of 1999. On days 1, 3, 8, 21, 28 and 42 of incubation, gas samples were collected and each jar ventilated with room air to replenish oxygen. Within 12 h, gas samples were analyzed for CO<sub>2</sub> content using thermal conductivity gas chromatography. A first order rate equation was used in non-linear regression analysis to calculate C pool size ( $\mu\text{g C/g dry soil}$ ) and a decomposition rate constant ( $\text{day}^{-1}$ ) from data on CO<sub>2</sub> flux over the incubation period (Townsend et al., 1997).

#### 3.6. Measurements of nitrogen dynamics

##### 3.6.1. Net mineralization and nitrification and soil inorganic N pools

Net mineralization and net nitrification rates were calculated as the difference between available N content at the beginning and end of 6-week incubations using the buried bag method (Eno, 1960). Incubations began in early spring and ended in mid to late fall, 1998. Since the ground freezes about 4 weeks earlier in the upper than in the lower reaches of Ward Creek, two incubations were performed in the upper reach plots (the Upper Meadow and Alder ecosystem types) and three were performed in the lower reach sites (the Transport, Depositional Willow and Depositional Meadow ecosystem types; Table 2). Four sub-samples were collected in each plot on each sample date. Sampled soils were kept cool until processed within 12 h. All soil extracts were immediately frozen until ready for analysis. Soil extract concentrations of ammonium and nitrate were measured on a Lachat autoanalyzer, as described above for groundwater samples. Soil from unincubated samples ( $t_0$ ) were used to measure N pools in 1998. During 1999, soil N pools were measured using the same methods described above except that these soil samples were from intact cores that had been used for 4 h acetylene block denitrification incubations (Merrill, 2001).

##### 3.6.2. Potential denitrification

Potential denitrification was measured using the denitrification enzyme activity (DEA) assay described by Smith and Tiedje (1979). Twenty-five grams of field moist soil (four homogenized replicates per site) were amended with 25 ml of a 1 mM KNO<sub>3</sub>/1 mM succinate solution in a 125 ml, stoppered Erlenmeyer. Each flask was flushed with N<sub>2</sub> for 4 min, and then further amended to 10 kPa CaC<sub>2</sub>-generated acetylene. Head-space was mixed thoroughly by pumping with a 40 ml syringe prior to collecting samples. The resulting soil slurries were incubated on a rotary shaker for 60 min at 20 °C. Gas samples were collected at 10, 20, 40 and 60 min and stored in the nylon syringes. Within 24 h, samples were analyzed for N<sub>2</sub>O content using electron capture gas chromatography.

#### 3.7. Statistical analysis

For each sample date, data on potential denitrification, net mineralization and net nitrification were analyzed using one-way analysis of variance with ecosystem type as a fixed main effect. In addition, potential denitrification, net mineralization and net nitrification rates were compared among ecosystem types while accounting for changes in season using two-way ANOVA in which ecosystem type and sample date were fixed effects. For all of these analyses, plot means were used to test for differences among ecosystem types. Tukey's multiple comparisons method was used to identify significant differences among pairs of ecosystem types after significant ANOVA tests. The significance of each one to one relationship between site characteristics (e.g. soil redox, moisture content, oxygen concentration, temperature, groundwater level, groundwater flux, microbially available C pool and decomposition rate, and soil ammonium and nitrate pools) and process rates (net mineralization, net nitrification, potential denitrification and groundwater DIN flux) was determined using correlation analysis (the coefficient of determination,  $R^2$ ). Step-wise linear regression was then used to identify the most important sets of correlates among those significantly correlated process rates and site characteristics. Significant correlations between more proximal and more distal hydrologic variables were also identified using the coefficient of determination ( $R^2$ ). Data were tested for normal distribution by examining skewness and kurtosis and data were tested for equality of variance using the Bartlett's test (Zar, 1999). Where appropriate, data were log-transformed to meet the assumptions of normality and equality of variance. To ease interpretation of results on log-transformed data, data means and standard errors were back-transformed to their original units before being presented in graphs and figures. S-PLUS Version 4.5 and JMP Version 3.2.1 software was used in order to perform these analyses.

## 4. Results

Potential denitrification rates averaged 17, 13, and 22.5 ng Ng<sup>-1</sup> min<sup>-1</sup> for all sites in 1997–1999, respectively. These rates are similar to those reported by Cosandy et al. (2003) for silty clay and silty sandy soils in riparian zones along

the River Morand in Switzerland (19.8 and 20.5 ng Ng<sup>-1</sup> min<sup>-1</sup>). But our rates are 10–100 times higher than those reported by Pinay et al. (2000) (1.2 ng Ng<sup>-1</sup> min<sup>-1</sup>), Ambus (1993) (0.8–0.3 ng Ng<sup>-1</sup> min<sup>-1</sup>), Groffman et al. (1992) (1.8 and 2.8 ng Ng<sup>-1</sup> min<sup>-1</sup>) and Lowrance (1992) (0.133 ng Ng<sup>-1</sup> min<sup>-1</sup>). Net mineralization rates measured in our study averaged 340 ng Ng<sup>-1</sup> day<sup>-1</sup>, while net nitrification rates averaged 360 ng Ng<sup>-1</sup> day<sup>-1</sup> for the 1998 growing season. These rates are comparable to those reported by others in mountain meadows and forested riparian zones (Fisk and Schmidt, 1996; Hanson et al., 1994; Groffman et al., 1996). In four of the five ecosystem types, net mineralization rates explained over 60% of the variation in net nitrification. Only in the Transport sites were these two processes apparently less tightly linked ( $R^2 = 0.35$ ).

#### 4.1. Ecosystem type differences

Significant differences in N process rates among ecosystem types across seasons and within seasons are presented in Tables 3 and 4. Across all seasons, differences among the five ecosystem types accounted for more variation in potential denitrification ( $aR^2 = 0.43$ – $0.52$ ;  $A > UM \geq DW \geq DM > T$ ) than in net mineralization ( $aR^2 = 0.12$ ;  $T \geq DW = A > DM > UM$ ) or in net nitrification ( $aR^2 = 0.27$ ;  $T \geq A = DW > DM > UM$ ).

Differences in site characteristics generally accounted for less variation in process rates than did differences in ecosystem type, except with regards to net nitrification. Within seasons, the amount of variation explained by ecosystem type was greater than the amount explained by site characteristics in half of the instances where differences were significant (Table 4). Nitrogen process rates varied independently among ecosystem types. For example, denitrification potential was often highest

in the alder meadows, whereas net mineralization was often highest in the Transport ecosystem type and lowest in the Depositional Meadow and Upper Meadow types (Fig. 3). Net immobilization was measured in the Upper Meadows during summer 1998 (Fig. 3).

Measured saturated hydraulic conductivity values ranged from 6.2 to 54.5 cm/h for these sites, a spread that includes rapid to very rapid conductivity rates (Black, 1965). Over the 1998 sampling season, the average calculated rate of groundwater flow ranged from 0.07 to 3.45 m<sup>3</sup>/h, and large differences in groundwater flow rates existed among ecosystem types. Ecosystem type explained 54% of the variation in flow rate among the all sites on all 1998 dates ( $p < 0.0001$ ). The ecosystem types were ranked in order of average flow rate as follows:  $T \gg A > DW = UM > DM$ . Flow through the Transport type was 10 times greater than in any other type, and flow through the Depositional Meadow type was one-half to one-quarter that of the other non-Transport types. We estimated the flow rate (flux) of groundwater inorganic N occurring at each site and sample date by multiplying site average groundwater N concentrations by site average groundwater flux. Two-way ANOVA, with ecosystem type and sample date as fixed effects, explained 42% of variation in groundwater DIN flux in the 20 sites over seven dates (Table 3). In all five ecosystem types, DIN fluxes peaked in late spring to summer and diminished in the fall (Fig. 4). Throughout the sampling season, DIN flux in the Transport type was significantly greater (e.g. more than double) than DIN flux in the rest of the ecosystem types studied (Fig. 4f). However, differences among the other types were also significant. The relative ranking of DIN flux in the ecosystem types was:  $T \gg A > DW \geq UM = DM$ .

The greatest differences in site physical conditions were often among ecosystem types, rather than among plots. During

Table 3  
Percent of variation in N dynamics and groundwater chemistry explained by ecosystem type and season (two-way ANOVA) vs. percent of variation explained by site characteristics (step-wise regression analysis)

N process	By ecosystem type and season		By site characteristics		
	$aR^2$	$p(F)$	$aR^2$	$p(F)$	Characteristics used
Net mineralization					
1998: 20 plots $\times$ 3 dates	0.12	0.036	No correlates		
Net nitrification					
1998: 20 plots $\times$ 3 dates	0.27	<0.001	0.37	<0.001	Soil redox (+), clay (+)
			0.56	<0.001	Net mineralization (+)
Potential denitrification					
1997: 20 plots $\times$ 2 dates	0.45	<0.001	0.35	<0.001	Soil moisture (+)
1998: 20 plots $\times$ 3 dates	0.43	<0.001	0.26	<0.001	Groundwater level (+) Soil oxygen (–)
1999: 20 plots $\times$ 2 dates	0.52	<0.001	0.80	<0.001	Soil moisture (+) Soil redox (–)
Groundwater DIN flux					
1998: 20 plots $\times$ 5 dates	0.54	<0.001	0.16	0.002	Silt (–)

Positive correlations reflect increased rates with increased values of each site factor, where high groundwater levels are closer to surface than low ones, and high redox levels are more oxidized than low ones.

Table 4

Percent of variation in N process rates explained by ecosystem type (one-way ANOVA) vs. by site characteristics (step-wise regression analysis) within seasons ( $n = 20$  for all analyses)

Season and year	By ecotype		By site characteristics		
	$R^2$	$p(F)$	$aR^2$	$p(F)$	Characteristics used
Net mineralization					
Spring 1998	Not significant		No correlates		
Summer 1998	0.37	0.03	0.22	0.050	Groundwater level (–)
Fall 1998 <sup>a</sup>	0.43	0.03	No correlates		
Net nitrification					
Spring 1998	Not significant		0.49	0.0003	Groundwater level (–)
			0.49	0.0003	Net mineralization (+)
Summer 1998	0.22	0.10	0.76	<0.0001	Net mineralization (+)
Fall 1998 <sup>a</sup>	0.31	0.05	0.54	0.03	Soil clay content (+), soil temperature (–)
			0.77	<0.0001	Net mineralization (+)
Potential denitrification					
Spring 1997 <sup>b</sup>	0.44	0.005	0.75	<0.0001	Soil moisture (+)
Summer 1997 <sup>b</sup>	0.47	0.006	0.17	0.04	Soil moisture (+)
Spring 1998	0.73	<0.0001	0.27	0.013	Soil silt content (+)
Summer 1998	None		0.23	0.018	NH <sub>4</sub> + N pool (+)
Fall 1998 <sup>a</sup>	None		No correlates		
Spring 1999	0.54	0.003	0.72	<0.0001	Soil moisture (+), groundwater level (+)
Summer 1999	0.50	0.005	0.74	<0.0001	Soil moisture (+), NH <sub>4</sub> + N pool (–)
Groundwater DIN flux					
Spring 1998	0.35	0.030	No correlates		
Summer 1998	0.54	0.008	0.32	0.010	Soil NO <sub>3</sub> -N pool (+)
Fall 1998 <sup>a</sup>	0.65	0.0007	0.64	0.004	Net mineralization (+), net nitrification (+)

<sup>a</sup> Net mineralization was not measured in the Alder or Upper Meadow ecosystem types during the fall of 1998, therefore this model only applies to the three other ecosystem types.

<sup>b</sup> No measures of site characteristics other than soil moisture were taken in 1997.

the spring and summer, average depth to groundwater was often greatest in the Transport ecosystem type. Groundwater was closest to the surface in the Depositional Meadow ecosystem type, but groundwater levels dropped quickly in both the Depositional Willow and Depositional Meadow types. Surface soil temperatures averaged 12 °C during July and August and differed among ecosystem types only during the fall (Fig. 5e). During 1998, differences in gravimetric soil moisture content among ecosystem types were significant in the spring, summer, and fall and roughly declined with elevation (Fig. 5b). In spring 1998, surface soil redox levels were lowest in the Upper and Depositional Meadow ecosystem types and highest in the Transport ecosystem type (Fig. 5d). Surface soil redox potentials varied widely in more oxidized soils (e.g. >200 mV), but pockets of reducing conditions appeared consistently in the Alder and Upper Meadow ecosystem types. Oxygen levels in the upper 10 cm of soil pore space were frequently just a few percent below ambient. Only in spring 1998, and then only in the Alder and Upper Meadow ecosystem types, were oxygen levels consistently well below 15% (Fig. 5a). Carbon pools ranged from 1000 to 5000 µg C/g dry soil. The largest pools of microbially available C were found in the Alder ecosystem type and the smallest pools were found in the Depositional Meadow ecosystem type. The inverse was true for decomposition rates. As the growing season

progressed, microbially available C pools increased while decomposition rates decreased in all types.

#### 4.2. Site correlates with N process rates

We examined correlations between environmental variables and process rates across versus within seasons and across versus within ecosystem types. In 1998, four processes were measured: net mineralization, net nitrification, potential denitrification and groundwater DIN flux. In 1997 and 1999, only potential denitrification was measured (see Table 2). The strongest site correlates, selected through step-wise regression analysis, often shifted as we moved from one framework to the next. For example, across all sites in 1998, potential denitrification was inversely correlated with soil oxygen and positively correlated with groundwater level (Table 3), but within ecosystem types, other site characteristics, such as soil temperature and microbial C pool came to the fore (Table 5). Similarly, the strongest site correlates with N process rates across all seasons were different than site correlates within seasons (Tables 3 and 4).

##### 4.2.1. Site correlates with N process rates across five ecosystem types

Through step-wise regression analysis, we found that gravimetric soil moisture and soil redox explained 80% of the

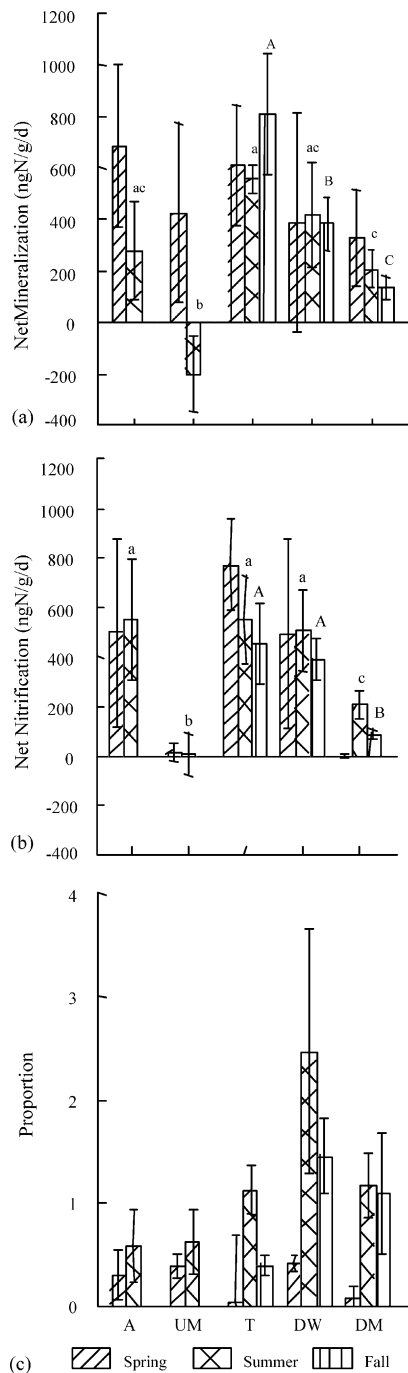


Fig. 3. Net mineralization, net nitrification and proportion of net mineralized N appearing as net nitrification during the 1998 field season. Ecosystem type means shown with one standard error. Significant differences among ecosystem types within seasons indicated with letters (one-way ANOVA, followed by Tukey's HSD test,  $p < 0.05$ ).

variation in potential denitrification during the 1999 field season ( $aR^2 = 0.80$ ,  $p < 0.0001$ ,  $n = 40$ , Table 3). In 1998, high groundwater levels and low soil  $O_2$ , rather than soil moisture content, explained 26% of variation in potential denitrification (Table 3). When site characteristics were examined within seasons, differences in soil moisture content and groundwater level explained over 70% of the variation in potential

denitrification during the springs of 1997 and 1999 (Table 4). Similarly, we found groundwater level to be an important correlate with net nitrification in the spring ( $aR^2 = 0.49$ ,  $p = 0.0003$ ,  $n = 20$ , Table 4). Along with soil clay content, soil temperature was strongly correlated with fall 1998 net nitrification rates (Table 4). In fall 1998, net mineralization and net nitrification rates were strongly correlated with groundwater N flux (Table 4).

#### 4.2.2. Site correlates with N process rates within ecosystem types

During 1998, the most important correlates with N process rates within an ecosystem type varied among types. For example, the decomposition rate constant was the most important correlate with net mineralization in the Upper Meadows, whereas gravimetric soil moisture content was the most important correlate with net mineralization rates in the Depositional Willows (Table 5). Soil moisture content was inversely related to net nitrification in the Alder and Depositional Willow ecosystem types (Table 5), whereas the microbial C pool was strongly correlated with nitrification in the Depositional Meadows ( $aR^2 = 0.45$ ,  $p = 0.041$ ; Table 5). Groundwater level was strongly correlated with 1998 potential denitrification in the lower elevation types, in which groundwater levels fall dramatically during early and mid-summer.

In contrast to 1998, 1999 site correlates to potential denitrification were consistent among ecosystem types: gravimetric soil moisture content was a common strong correlate with potential denitrification among all but the Upper Meadow ecosystem types (Table 5). No significant correlates with potential denitrification were measured in the Upper Meadow type during 1998 and 1999, suggesting that some other unmeasured factors might be more important.

Groundwater DIN flux was negatively correlated with soil redox in the Depositional Willow ecosystem type (Table 5); none of the site physical characteristics measured were correlated with groundwater DIN flux in the other four ecosystem types.

## 5. Discussion

Ecosystem type differences were significant for all N process rates measured, including net mineralization, net nitrification, potential denitrification and groundwater DIN flux. However, the relative ranking by process rate among ecosystem types differed for each process, e.g.  $A > UM \geq DW \geq DM > T$  for potential denitrification and  $T \geq DW = A > DM > UM$  for net mineralization. Therefore, any simplified grouping of the 20 research plots, for example, with and without alders, or according to valley width, would lump into one group several plots which differ significantly in at least one process rate. Thus, important information would be lost by further simplifying the ecosystem type groupings of the 20 study plots. Although some of the environmental characteristics were, during some seasons, highly correlated with some process rates (e.g. soil moisture content and potential

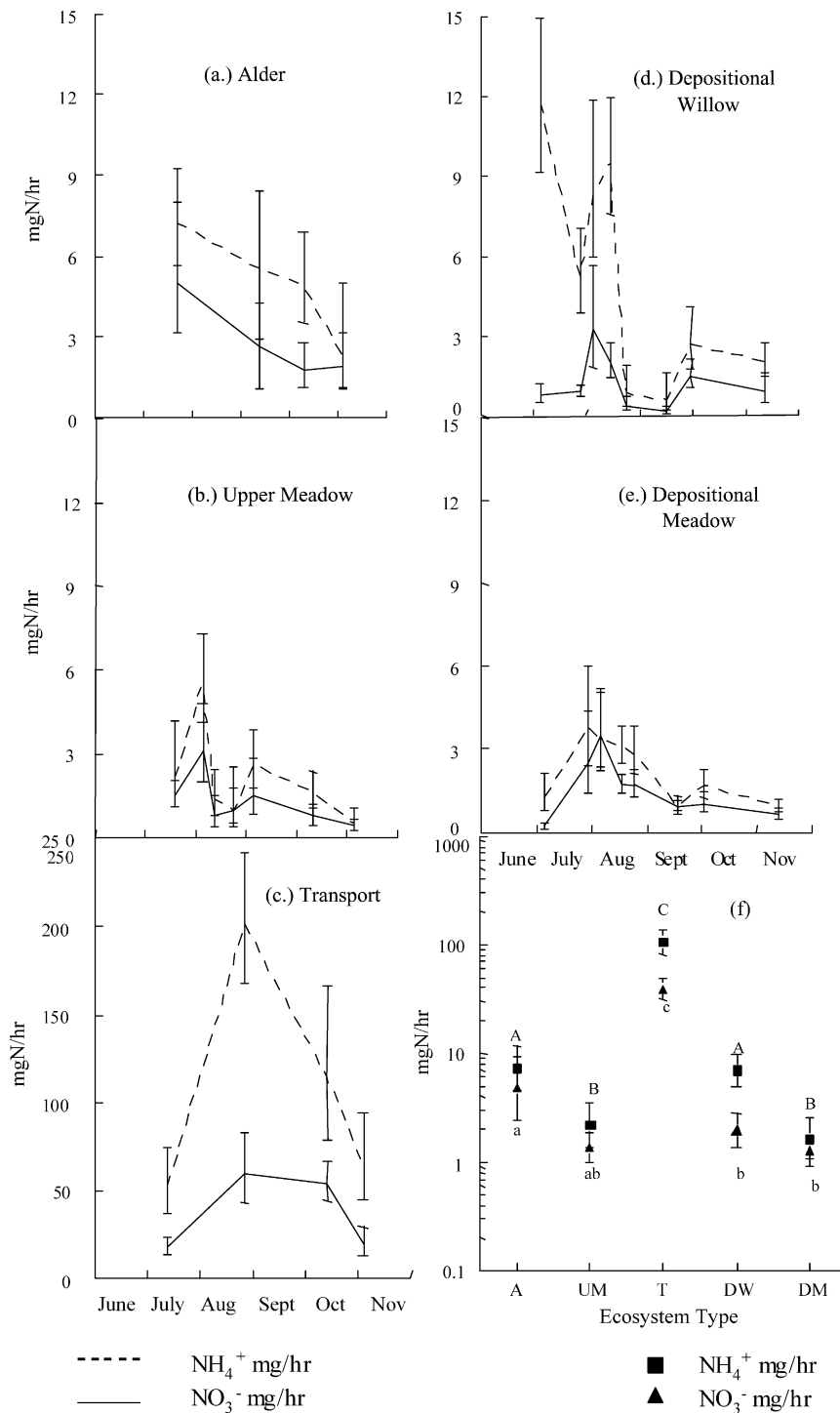


Fig. 4. Flux in groundwater  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  in each ecosystem type (a–e) during 1998 field season. Groundwater N flux in each ecosystem type, averaged over all sample dates, are presented in (f); note that y axis on (f) is log scale. Significant differences among types indicated by different letters (Tukeys HSD,  $p < 0.05$ , following significant two-ANOVA test). Ecosystem type means  $\pm 1$  S.E. shown.

denitrification during 1999), no single characteristic was consistently correlated with all or even two process rates. Thus, in this study, ecosystem type proved to be the most ‘universally’ informative physical characteristic regarding differences in N process rates among riparian sites.

Variation explained by ecosystem type overlapped with that explained by the site characteristics: site correlates were always

insignificant in the presence of ecosystem type in standard least squares linear regression models. Therefore, roughly 50–70% of the overall variation in N process rates among the 20 study sites was unexplained by either ecosystem type or the site characteristics as measured. Unaccounted for variation could be due to differences among plots, within ecosystem types, of some unmeasured variables (e.g. plant uptake), and/or short-

Table 5

Percent variation explained by site characteristics, selected through step-wise regression analysis, in N process rates within ecosystem types ( $n = 12$ )

Type	Correlates	aR <sup>2</sup>	p(F)
Net mineralization 1998			
A	No correlates		
UM	C decomposition rate constant, $k(+)$	0.74	0.004
T	No correlates		
DW	Soil moisture content (–)	0.78	<0.001
DM	Soil sand content (–)	0.30	0.047
Net nitrification 1998			
A	Soil moisture content (–), sand content (+)	0.88	0.002
	Net mineralization (+)	0.60	0.015
UM	Net mineralization (+)	0.68	0.004
T	Net mineralization (+)	0.35	0.025
DW	Soil moisture content (–)	0.74	<0.001
	Net mineralization (+)	0.94	<0.001
DM	Microbial C pool $a(+)$	0.62	0.012
	Net mineralization (+)	0.88	<0.001
Potential denitrification 1998			
A	Soil temperature (+), soil O <sub>2</sub> (–)	0.81	0.007
	Net nitrification (–)	0.66	0.009
UM	None		
T	Microbial C pool, $a(+)$	0.45	0.041
	DIN flux (+)	0.78	<0.001
DW	Soil temperature (+)	0.26	0.052
	Groundwater level (+)	0.26	0.053
DM	Groundwater level (+)	0.46	0.010
	Soil temperature (+)	0.33	0.030
Potential denitrification 1999			
A	Soil moisture (+)	0.71	0.010
	Redox (–)	0.62	0.020
UM	None		
T	Soil moisture (+)	0.63	0.011
DW	Soil moisture (+)	0.98	<0.0001
DM	Soil moisture (+)	0.80	0.002
Groundwater DIN flux 1998			
A	None		
UM	None		
T	None		
DW	Soil redox (–)	0.57	0.003
DM	None		

Measurements of soil temperature, groundwater flux and net nitrification/mineralization were not taken in 1999.

comings in our measurement methods (e.g. soil redox is notoriously difficult to measure in the field).

Our findings on N process rates show the *relative* importance of different N processes in the five ecosystem types studied; the measures we made of the processes were imperfect and under more idealized conditions than occur in situ. For example, the buried bag technique works well to indicate net microbial DIN release in soil where the soil moisture is held constant and plant uptake and exudates are excluded for the duration of the incubation, not as a measure of actual field DIN availability.

Similarly, the denitrification potential assay reflects denitrifier enzyme activity in the soil at the time of sampling, not in situ rates of denitrification. Therefore, management implications of our findings are best made by considering the relative importance of each process, and the possible (measured and unmeasured) controls on these rates.

### 5.1. Physical site correlates with N process rates

#### 5.1.1. Net mineralization and net nitrification

Measures of the aerobic processes net mineralization and net nitrification were most strongly correlated with indicators of soil moisture (soil moisture and groundwater level) and microbially available C (C decomposition rate constant, Tables 3–5). Similarly, Groffman et al. (1996) report that groundwater level and soil organic matter content were the best predictors of net mineralization in four distinct northeastern wetland types. In our study, indicators of moisture, such as groundwater level and gravimetric soil moisture content, were strongly inversely correlated with net mineralization and nitrification in the shrub types, while microbially available C was strongly correlated with net mineralization in the Upper Meadow type. These findings indicate that aerobic conditions could be most limiting in the shrub sites, while microbial activity is most limited by C rather than soil saturation in the Upper Meadows. Similarly, Fisk and Schmidt (1996) found that microbial N uptake increased toward the end of the growing season when there was the greatest microbial C available (due to the flush of available C from senescing vegetation). Net immobilization was only measured in the Upper Meadows during the summer (Fig. 3a). These results suggest that, except for the Upper Meadows in the summer time, microbial immobilization is not likely to be a large sink for added N in these ecosystem types.

Since nitrifiers are chemoautotrophs, the correlation between microbially available C pools and net nitrification rates in the Depositional Meadows is unexpected, and could reflect covariation with some unmeasured variable(s). Nitrifying bacteria use oxygen (O<sub>2</sub>) as a final electron acceptor (Paul and Clark, 1989). As a result, high oxygen availability, as reflected in well-oxidized soils, facilitates nitrification. Therefore, it is surprising that soil oxygen concentration was not correlated with nitrification rates as well as soil redox (Table 3). These results may be due to incomplete sampling of soil oxygen levels. Approximately half of the soil atmosphere chambers were replaced (and therefore not sampled) in the lower sites in the spring of 1998, when the greatest variation in soil oxygen concentration occurred. By missing this broader range of oxygen conditions, a significant correlation between oxygen and nitrification rates may not have been discernable.

#### 5.1.2. Potential denitrification

Our findings that gravimetric soil moisture content was a primary correlate with potential denitrification are similar to those reported by others (Parsons et al., 1991; Ambus, 1993; Pinay et al., 2000). Others report correlations between

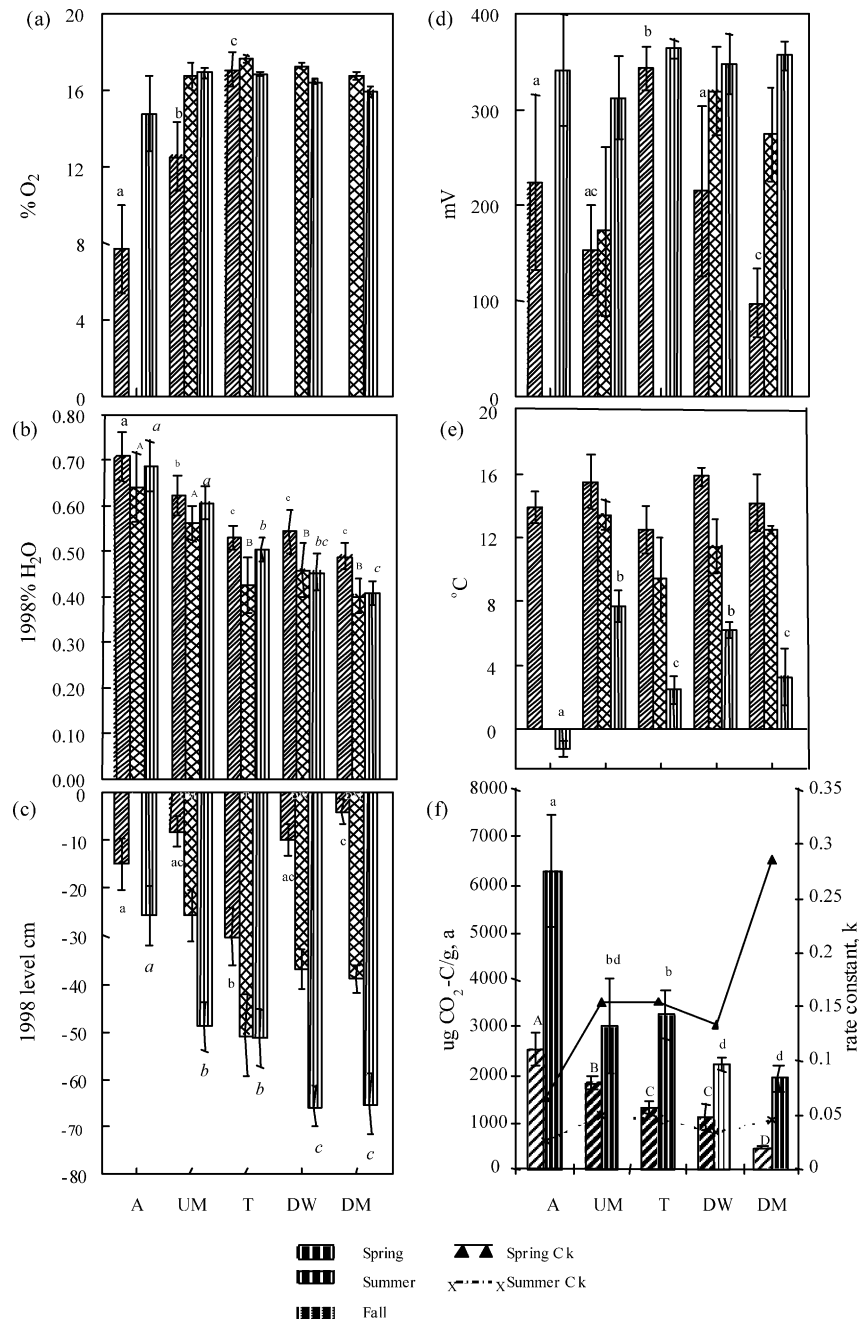


Fig. 5. Surface soil conditions in 20 riparian sites in Lake Tahoe Basin during the snow-free season of 1998, except microbially available C (Fig. 10f), which was measured in 1999. Ecosystem type averages, calculated from plot means, shown with 1 S.E. for spring, summer and fall. (a) Surface soil oxygen content, (b) surface soil moisture content, (c) groundwater levels, (d) surface soil redox, (e) surface soil temperature and (f) surface soil microbially available C pools (bars) and decomposition rate constants (lines). Ecosystem type differences within a season indicated by different letters of same font (Tukey's HSD).

denitrification and soil moisture content in soils with over 60% soil moisture (Groffman and Tiedje, 1991; Parsons et al., 1991). During 1998 field season this relationship did not hold true for those sites with over 60% soil moisture. However, during 1999, denitrification potential was correlated with soil moisture in areas with over 60% soil moisture content as well as across the entire range of soil moistures measured (40–85%; Table 3). Although soil moisture was clearly the most important site correlate with potential denitrification during 1999, groundwater level and soil oxygen concentration were also strong correlates with potential denitrification in 1998 (Tables 3 and

4). All of these factors, including soil oxygen concentration, redox, soil moisture content and groundwater level, could reflect underlying constraints on denitrification due to availability of anaerobic conditions.

It is unclear why apparent controls on anaerobic conditions would vary from 1 year to the next. Differences in weather patterns among 1997–1999 may have influenced the observed differences in correlates with potential denitrification during these years (Table 5). Although above average precipitation occurred during all 3 years of this study, the distribution of precipitation varied from year to year. The spring snowmelt

period in 1998 extended 3–4 weeks later than the other 2 years, making spring 1998 particularly wet. Mid-summer precipitation was very low in 1997, moderate in 1998 and high in 1999 (Merrill, 2001). Thus, 1997 and 1998 had wet springs and dry summers, while 1999 had a dry spring and rainfall nearly  $2.5\times$  that of normal in August (Merrill, 2001). The potential denitrification assay tests for activity of the denitrifier enzyme: a metabolic product made in response to conditions conducive to denitrification. Smith and Parsons (1985) found that these enzymes persist for weeks in air-dried soils and suggest that fluctuations in soil moisture content might trigger the activation–deactivation of existing denitrification enzymes. Thus, it is possible that moisture that spurred production/activation of the denitrifier enzymes was still present in soils sampled in late August and early September of 1999, but the dry summers of 1997 and 1998 may have depleted all microsites of soil moisture, resulting in little temporal or spatial variation in effective moisture availability. We measured strong correlations between soil moisture content and soil texture, but not between soil moisture and groundwater level, in 1999. In 1998, however, groundwater level and soil moisture were correlated ( $R^2 = 0.28$ ,  $p < 0.01$ ; Merrill, 2001). This supports the interpretation that in 1999, soil moisture was primarily delivered via rainfall, whereas in 1998, mid-summer soil moisture was derived primarily from groundwater (snowmelt).

Under the dry weather conditions of 1998, site characteristics most highly correlated with denitrification potential varied by ecosystem type (Table 5). For example, groundwater level was highly correlated with potential denitrification in the Depositional Meadows, but not in the Alders, where surface soil temperature and oxygen were most closely correlated with denitrification potential rates. Groundwater levels were consistently high in the Alder sites; however, this water was variously aerated, sometimes gurgling close to the surface, other times flowing through a rich organic layer several inches below ground. Thus, in the Alder ecosystem type, level to groundwater might not reflect the extent of anaerobic conditions as accurately as soil oxygen. In contrast to the Alders, groundwater levels dropped dramatically in the Depositional Meadow sites as the 1998 summer progressed, and thus did provide a strong indicator of aerobic conditions. As with net mineralization, these results suggest that factors that control the distribution of anaerobic conditions, a proximal controller of denitrification, can vary by ecosystem type. Other possible proximal control factors, including C and  $\text{NO}_3\text{-N}$  availability, were not correlated with denitrification potential except for in the Transport sites in 1998 (Table 5). These findings suggest that  $\text{O}_2$  availability might be the most important proximal controller of denitrification in these riparian systems and that more distal controls over  $\text{O}_2$  availability differ among ecosystem types, seasons, and even years (Fig. 1).

### 5.1.3. Groundwater DIN flux

Groundwater N flux (mg N/h) reflects the amount of N in groundwater that was passing through the site at the time of sample collection. If one assumes that the chemistry of

groundwater entering the riparian zone is similar across all 20 sites, then site differences in groundwater N flux should reflect riparian effects on groundwater N. There is some evidence to suggest that the N chemistry of the incoming groundwater should be similar across ecosystem types in Ward Creek Basin. The uplands surrounding Ward Creek are primarily Forest Service land with second growth and old growth upper montane forests. Some housing development has occurred in the watershed, but the nearest residence is over 2000 m away from the valley floor. In addition, all sewage in the Tahoe Basin has been exported, since 1970 (State Water Resources Control Board, 1980).

The major possible upland N sources include atmospheric deposition and N fixation. It is possible that atmospheric N deposition could vary at different elevations in the watershed, and because the ecosystem types are not randomly distributed throughout the watershed, different ecosystem types could be experiencing different amounts of added N. Jassby et al. (1994) found that the greatest amount of N deposition occurred as wet deposition during the rain and snow season (e.g. late October–June). Winter inversions trap local sources of N below about 2200 m. The resulting elevational gradient in N deposition would diminish rather than exaggerate the differences in groundwater N flux observed in the higher elevation Alder and Transport sites. Moreover, the Alder and Upper Meadow sites, with relatively high and low flux rates, respectively, frequently occur adjacent to one another, and are therefore very likely to be receiving groundwater with similar chemistry from the surrounding uplands. Patches of N fixing symbionts could also affect groundwater N levels. Thinleaf alders (*Alnus incana* ssp. *tenuifolia*) are the most common N fixing symbionts in the watershed, and occur primarily in the Transport and Alder meadow ecosystem types. Snow bush (*Ceanothus cordulatus*) is also an N fixing symbiont and grows intermittently in the forests of Ward Creek watershed. However, due to its sparse cover, the groundwater N contribution from this species is likely to be small. In summary, it is possible that the incoming groundwater N content is similar across ecosystem types, particularly between the Upper Meadow and Alder types; however, many measurements of upland groundwater chemistry around the watershed would be needed to prove this was the case.

Groundwater DIN flux was an order of magnitude greater in the Transport ecosystem type than in the other sites. This difference is largely due to differences in groundwater flux ( $Q$ ); the  $aR^2$  between  $Q$  and DIN flux for all sites and dates in 1998 was 0.81,  $p < 0.0001$  (Merrill, 2001). Groundwater flux is a function of soil texture and hydraulic head. Since differences in soil texture among ecosystem types were relatively minor compared to differences in groundwater flux, we suspect that flow rate differences were primarily controlled by differences in hydraulic head. Others (Hill et al., 2000; Hedin et al., 1998) have found that groundwater flows in C-rich sediment can foster high rates of groundwater N loss through denitrification. Similarly, pools of microbially available C and DIN flux rates were both positively correlated with denitrification potential in the Transport sites ( $aR^2 = 0.45$ ;  $aR^2 = 0.78$  Table 5).

In the Transport ecosystem type, potential denitrification was strongly correlated with groundwater DIN flux in 1998 ( $aR^2 = 0.78$ ,  $p = 0.0002$ ,  $n = 12$ ; Table 5). Groundwater DIN flux was not correlated with denitrification potential in any of the other four ecosystem types. These results could reflect a causal relationship between groundwater DIN flux and potential denitrification: ground and surface water could carry enough nitrate from N fixing alders to fuel high denitrification rates. However, further research would be required in order to determine whether there actually is a causal link between denitrification potential and DIN flux in the Transport ecosystem type, or if the high correlation was due to co-variation with some other unmeasured variable, such as seasonal variation in plant uptake.

N supply also seemed to be an important controller of groundwater N flux. Factors controlling soil N availability, including soil N pool, net nitrification and net mineralization rates, were correlates to DIN flux in the summer and fall, but not spring, of 1998. Thus, the effects of biological processes on DIN flux could become increasingly important as the growing season progresses.

## 5.2. Management implications

Results from this research can be applied to gain insight on N dynamics specific to the five ecosystem types studied. Potential denitrification rates were highest in the spring and summer and most strongly correlated with soil moisture content and/or availability of anaerobic conditions. High soil moisture and anaerobic conditions are likely to be most common during the period of spring snowmelt, the same period during which the largest flush of N enters the tributaries to Tahoe (Leonard et al., 1979; Coats and Goldman, 1993). The coincidence of peak denitrification potential and spring snowmelt suggests that riparian N removal via denitrification could play a role in the annual N budget of these watersheds. However, DIN flux measurements were several orders of magnitude higher than potential denitrification rates, which are likely to be far higher than in situ rates. Furthermore, others have reported that DIN in the snowpack elutes out at the very earliest period of snowmelt (Williams and Melack, 1991), a period during which we did not measure denitrification potential.

However, if groundwater rich in DIN flows through a large area of riparian zone, denitrification effects could accumulate across the full length of the flow path, and thereby reduce groundwater DIN levels. These conditions would require a fairly wide riparian zone, in which the groundwater stays close to the surface so that surface soil denitrifiers could access groundwater nitrate. These conditions are most likely in the Upper Meadow and the Depositional Meadow ecosystem types. Net mineralization rates also peaked during the spring in these two ecosystem types. A similar seasonal pattern of high spring N availability was reported for alpine sedge meadows at Niwot Ridge (Fisk and Schmidt, 1995), where measures of plant N uptake peaked in the spring (Jaeger and Monson, 1992). Although we did not measure plant uptake, rapid plant growth was observed in these sites during spring measurements (Merrill, personal observation).

High rates of plant uptake coupled with denitrification during the spring could also explain low spring DIN flux in the Upper and Depositional Meadows despite relatively high mineralization rates. Results from this research also suggest that N could be both immobilized and significantly removed via denitrification from the Upper Meadow sites in late summer (August 1998; Figs. 4 and 6). Low groundwater DIN flux measured in the Upper Meadow sites during the spring and late summer support this interpretation (Fig. 4).

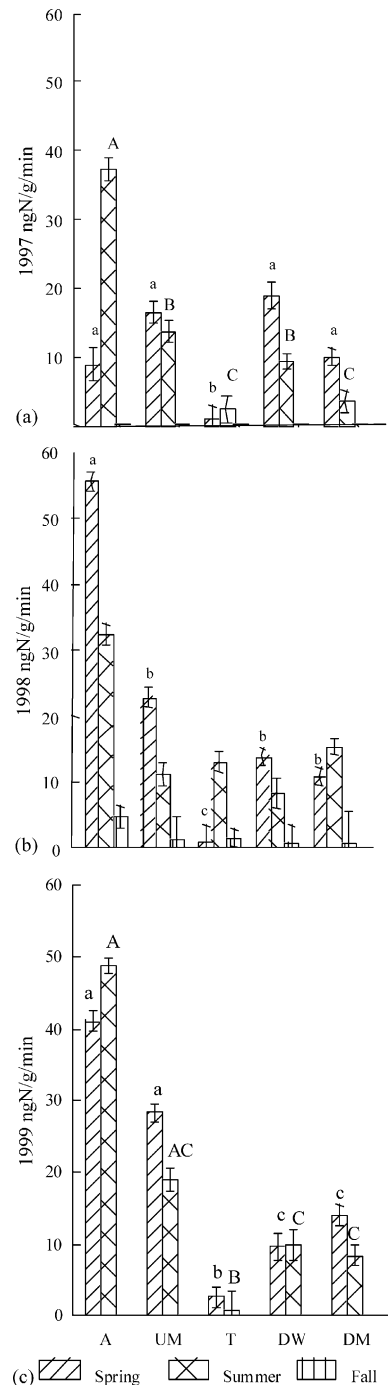


Fig. 6. Potential denitrification during seasons of 1997–1999. Graphs show ecosystem type means  $\pm$  1 S.E. Letters indicate significant differences in paired post hoc comparisons (Tukey's HSD,  $p < 0.05$ ) following significant one-way ANOVA tests among ecosystem types within each season.

The Depositional Meadow and Depositional Willow ecosystem types behaved in a roughly similar fashion during our time of study. These systems occur in the lower reaches of the watershed and are subject to the same seasonal groundwater draw down as the wet spring turns to dry summer. Denitrification potential was high during the moist spring period when the groundwater is high enough to saturate the rooting zone. We did not measure plant N uptake, but observed very rapid plant growth in the early spring in the Depositional Meadows; like the Upper Meadows, this could also be an important early season vector of soil and groundwater N removal. Potential denitrification rates decreased in these systems as groundwater levels receded during the later half of the summer. Thus, both of these lower reach ecosystem types could remove some N from ground and surface water during the early part of the season, but are not likely to affect ground or surface water N later in the growing season.

The Alder ecosystem type had high potential denitrification rates and relatively high net mineralization and nitrification rates. Water flowed through the Alder surface soil all summer from high elevation snow fields, maintaining reduced conditions and high denitrification potential more consistently than in the other ecosystem types. However, the large N pools in this ecosystem type and high coverage of an N fixing shrub (Alder), could make these sites N sources to the ground and surface water throughout the snow-free season. Since the Transport ecosystem type also had high net mineralization and net nitrification rates, and large N pools (Fig. 3), but low denitrification potential (Fig. 6), they are a likely source of stream nitrate, particularly during spring snowmelt and fall rains. Our measure of groundwater DIN flux, which was roughly an order of magnitude greater in the Transport than in the other sites, supports this interpretation. This ecosystem type is common in the Tahoe Basin, and might be an important source of N for the aquatic food web in many of the tributary streams.

Others have also reported evidence that alder-rich thickets might act as N sources in the watershed due to assumably high fixation rates and the relatively high N content of alder litter (Kiernan et al., 2003; Coats, 1975; Goldman, 1961). However, the difference in DIN flux from the two alder-dominated ecosystem types (the Transports versus the Alders) indicates that characteristics other than vegetation affect groundwater DIN flux. The higher denitrification potentials coupled with the lower flux rates and longer flow paths in the Alder sites compared to the Transport sites might explain the difference in nitrate fluxes between these two alder-dominated ecosystem types. As demonstrated by Tables 3–5, site factors other than measures of N availability can limit potential denitrification rates. For example, in the Transport sites microbially available C and temperature were more highly correlated to potential denitrification than measures of N availability (Table 5). Similarly, differences in denitrification potential among ecosystem types were more highly correlated to soil moisture and O<sub>2</sub> content than to measures of N availability (Table 1). Thus, ecosystems rich in N fixing species must be expected to vary in denitrification and other microbial N process rates, since some process constraints can be as important than substrate availability.

Thus, in Ward Creek, we found that alder thickets along steep stream reaches (the Transport ecosystem type) are more likely than the alder meadows (the Alder ecosystem type) to be important sources of ground and surface water N. This contrast between the Alder and Transport ecosystem types demonstrates the importance of viewing areas in the riparian zone as integrated ecosystems in which the soil, vegetation and hydrology must be considered together in order to understand their existing conditions and to possibly predict their responses to change.

## 6. Summary

Our findings that N process rates differed significantly among ecosystem types suggest that ecosystem types can be used to distinguish areas in the riparian landscape with different functional attributes. These results suggest that once riparian ecosystem types have been identified and mapped, land managers could use this information to gain insight on spatial variation in riparian processes, such as ground and surface water N inputs and removal. The primary correlates to potential denitrification, net mineralization and nitrification and groundwater DIN flux often changed when we shifted focus from all ecosystem types to within ecosystem types or from all seasons to within seasons. Others have reported similar shifts in apparent process controls with changes in scale (Sollins et al., 1983; Neilson and Wullstein, 1983; Magnuson et al., 1990). Our results suggest that the more distal factors controlling N processes can differ among ecosystem types. This indicates that construction of spatially explicit models of riparian function might be most accurately and effectively done by viewing the riparian landscape as an area containing several different ecosystem types, each with characteristic pathways of control, rather than as a single, uniform swath of land adjacent to a river or stream.

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